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An fMRI study of finger tapping in children and adults

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Abstract

Functional brain imaging studies have characterized the neural bases of voluntary movement for finger tapping in adults, but equivalent information for children is lacking. When contrasted to adults, one would expect children to have relatively greater activation, reflecting compensation for an underdeveloped motor system combined with less experience in the execution of voluntary movement. To test this hypothesis, we acquired functional magnetic resonance imaging (fMRI) data on 17 healthy right-handed children (7.48 ± 0.66 years) and 15 adults (24.9 ± 2.9 years) while they performed an irregularly paced finger-tapping task in response to a visual cue (left- and right-hand examined separately). Whole-brain within-group analyses revealed that finger tapping in either age group and for either hand activated contralateral SM1, SMA, ipsilateral anterior cerebellum, and occipital cortices. We used an ANOVA factorial design to test for main effects of Age Group (children vs adults), Hand (left vs. right), and their interactions. For main effects of Age Group, children showed relatively greater activity in left SM1 (extending into bilateral SMA), and, surprisingly, adults exhibited relatively greater activity in right pre-SMA/SMA (extending into left pre-SMA/SMA), right lateral globus pallidus, left putamen, and right anterior cerebellum. The interaction of Age Group × Hand revealed that while both groups activated right SM1 during left finger tapping and exhibited signal decreases (i.e., below fixation baseline) during right finger tapping, both these responses were attenuated in children relative to adults. These data provide an important foundation by which to study children with motor disorders.

KEYWORDS
child, functional neuroimaging, hand, humans, magnetic resonance imaging, movement

1 | INTRODUCTION

Owing to their simplicity of construct and execution, and their utility in assessing motor function in health and disease, finger-tapping paradigms have long been used in neuroimaging studies for probing motor substrates. The results of 38 of these studies have been summarized by an activation likelihood estimate (ALE) meta-analysis, which investigated regions in the adult brain that underlie finger tapping under differing task complexity and stimulus modalities (Witt, Laird, & Meyerand, 2008). The meta-analysis found that for right hand index finger movement (a smaller subset of the larger meta-analysis), activation is likely found in left primary sensorimotor cortex (SM1), supplementary motor area (SMA), ventral premotor cortex (PMv), basal ganglia, as well as bilateral anterior cerebellum, claustra, dorsal premotor cortex (PMd), and dorsolateral prefrontal cortex (DLPFC) and right inferior parietal lobule (IPL), insula, and inferior frontal gyrus (IFG).

In contrast to a large number of publications on finger tapping in adults, few functional magnetic resonance imaging (fMRI) studies have examined the functional anatomy of finger tapping in healthy developing children (De Guio, Jacobson, Molteno, Jacobson, & Meintjes, 2012; Du Plessis et al., 2015; Mostofsky et al., 2006; Rivkin et al., 2003; Roessner et al., 2012, 2013; Vandermeeren et al., 2003). Characterizing the brain regions that subserve finger tapping in typical children is important, firstly, because it can be contrasted to adult data, thereby contributing to the growing developmental literature on sensorimotor processing; and secondly, because it provides normative data by which to consider childhood disorders of motor control (e.g., cerebral palsy) and other disorders with associated motor impairments (e.g., developmental dyslexia and autism spectrum disorders). Of the studies published to date, one focused on healthy children only (Rivkin et al., 2003), and others compared healthy children to children with disorders (Du Plessis et al., 2015; Mostofsky et al., 2006; Roessner et al., 2012, 2013; Vandermeeren et al., 2003). Only one study directly contrasted children and adults (De Guio et al., 2012).

In the study by Rivkin et al. (2003), children performed two experiments: one using externally paced (auditorily) and the other internally paced bimanual movement, whereby the left hand alternated with the right hand during finger tapping. The resulting maps for the externally paced condition showed activation in bilateral posterior superior temporal gyrus, SM1, SMA, and cerebellum; and maps for the internally paced condition showed activation in bilateral SM1, SMA, pre-SMA, and cerebellum. The results were interpreted in the context of the adult published literature as no data were acquired in adults for direct comparison. Using this approach, the authors speculated that SMA is uniquely recruited by children for externally paced movement and pre-SMA is uniquely recruited by children for internally paced movement. De Guio et al. (2012) compared children with adults during rhythmic finger tapping. In their study, subjects began with dominant hand finger tapping in (regular) pace with an auditory stimulus (metronome) and then were asked to maintain the exact rhythm after the pacing stimulus was removed. Only those blocks in which there was no longer external pacing were used as a contrast with rest blocks and only if the subject had accurately maintained the rhythm. Activations for this comparison, which was designed to focus specifically on timing, were observed in children in left SM1, premotor cortex, thalamus, and claustrum; and bilateral cerebellum and occipital cortex. Of note, pre-SMA, which was emphasized by Rivkin et al. (2003) to be important for children during internally paced movement, was not activated. De Guio et al. (2012) also studied adults, but activation patterns were, as the authors described, unexpected, with activation in motor cortical areas evident only at a very lenient threshold ($p_{\text{uncorrected}} < .05$). Nevertheless, a between-group comparison revealed that children had greater activation than adults in bilateral SM1, cerebellum, and occipital cortex; left premotor cortex and middle temporal gyrus; and right thalamus. These findings support the idea that children, perhaps due to their immature motor system and lack of experience, require more activity than adults to perform the task.

Here, we compared children and adults, this time using a more commonly used task involving externally, and not internally paced, finger tapping. We also acquired data separately for left hand finger tapping and right hand finger tapping, to test for hand-dependent differences in activation between children and adults. While there have been reports to suggest that age-related differences in performance of simple tasks (pressing a button as fast as possible) do not depend on left or right hand use, specifically (Carlier, Dumont, Beau, & Michel, 1993; Tinker and Goodenough, 1930), the role of hand (left or right) has been shown to be important for a more complex task, such as moving pegs (Roy, Bryden, & Cavill, 2003). Therefore, in a study of children and adults tapping either hand, one might expect to see a main effect of hand (left versus right finger tapping), and perhaps also an interaction of age by hand.

Based on this, our goals were twofold: first, to characterize the motor system in children alone and second, to compare children and adults, thereby contributing to the developmental literature on sensorimotor processing. We expect more brain activity in children to compensate for poorer performance and less experience. This may be especially pronounced in SMA, as suggested by Rivkin et al. (2003), but also more widespread than this, involving multiple regions as reported by De Guio et al. (2012). We also expected the differences to be more pronounced in the hemisphere ipsilateral to the movement when using the nondominant hand (i.e., left hemisphere). To test these predictions, we generated group maps for right-handed children and adults performing right hand as well as left hand finger movement separately in response to an externally, irregularly paced stimulus. Next, we tested for age-specific between-group differences; specifically, we expected greater activity and more recruitment of neural resources in children than adults. Finally, given the full-factorial nature of our data, we also conducted a 2×2 Analysis of Variance (ANOVA), which allowed us to test whether there were main effects of age and/or hand, and whether age-related differences depend upon hand use, as would be indicated by an interaction.

2 | METHODS

2.1 | Participants

All subjects were typical, healthy individuals with no history of neurological disease or learning disability. We assessed intelligence quotient (IQ) in all participants using the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999) to ensure children and adults had an IQ above a standard score of 85 and were matched on this measure. All subjects were right-handed (Edinburgh Handedness Inventory; Oldfield, 1971). FMRI data were collected on 19 children and 17 adults during left hand and right hand thumb tapping. Both children and adults participated in additional scans and partly overlap with the subjects reported in previous work from this lab (Olulade, Flowers, Napoliello, & Eden, 2013).

2.2 | fMRI task and acquisition parameters

During functional data acquisition, subjects performed a visually paced, unimanual finger-tapping task. One run required finger movement of the left hand and the other run required finger movement of the right hand. Run order was randomized. Subjects were instructed to press the button with their thumb in response to a circle surrounding a cross (plus sign). The tasks were presented using a block design (Figure 1), which consisted of 4 tapping blocks (Tap) interspersed with fixations (Fix). For the fixation condition, the cross was omnipresent throughout the acquisition period and subjects were asked to keep their eyes fixated on the cross at all times. Finger-tapping stimuli were indicated by the addition of a circle surrounding the cross. All Tap blocks were 24 seconds. Within these blocks, the timing of the stimulus presentations varied and a 100 ms Tap stimulus appeared at one of three intervals: once per 650 ms, once per 900 ms, or once per 1,150 ms. Each interval was used 8 times per block and interval order was randomized and differed for each Tap block. For each run (one left hand, one right hand) we acquired 8 volumes from each of the four Tap blocks (32 Tap volumes) and each of the four Fix blocks (32 Fix volumes). We also acquired three additional Fix volumes at the beginning of the run, which were discarded from the analysis to reduce T1 saturation effects.

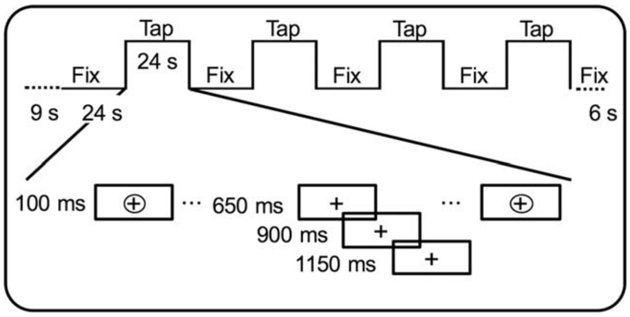

FIGURE 1 fMRI task presented in block design. Blocks of tapping are interspersed with blocks of fixation

Visual stimuli were generated using Presentation software, which fed into a screen behind the scanner that subjects could view from inside the scanner using an angled mirror apparatus fastened to the head coil.

To familiarize subjects with the scanner environment and to reduce learning effects, subjects practiced each task before entering the real scanner. To minimize head motion and ensure comfort during the actual scan, we placed foam cushions on both sides of the subject's head and around their arms. Although the tasks were relatively simple, we made accommodations for the children to mitigate any anxiety around the scanner. Children lay in a mock scanner prior to the real scan, and for the real scan, the scanner was decorated with a castle façade and children were offered Medieval Period costumes to wear.

Functional images were acquired on a 3 T Siemens Trio scanner. Functional EPI volumes were acquired with blood-oxygen-level dependent (BOLD) contrasts, using TR = 3,000 ms, TE = 30 ms, 50 axial slices, each of 2.8 mm, acquired anterior to posterior, sequentially, with a 0.2 mm gap, 192 mm field of view, and a 64×64 matrix, resulting in 3 mm isotropic voxels.

2.3 | Analysis of behavioral data

From the in-scanner log files, we calculated three performance measures: (a) false presses, defined as the sum of the number of button presses exceeding the required single press for each tap trial; (b) accuracy, defined as the percent of trials in which subjects pressed the button when prompted; and (c) response times, defined as the time between the onset of the circle around the fixation cross and the subject's button press; response times were calculated from correct as well as incorrect responses. For one adult subject, in-scanner log files were lost; thus, for the data used in subsequent fMRI analyses (covariates, see below), their summary performance measure was replaced with the group-averaged value.

2.4 | Analysis of fMRI data

The 64 volumes from each run were preprocessed and analyzed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). Preprocessing comprised three major steps: realignment of volumes to correct for head motion throughout the run, normalization to the Montreal Neurological Institute (MNI) EPI template with an isotropic 2 mm voxel size to correct for intersubject spatial variability, and smoothing to an isotropic 8.0 mm Gaussian kernel to improve the signal-to-noise ratio. Following the preprocessing procedure, smoothed images were overlain with the MNI template to ensure successful normalization.

We undertook several additional steps to account for head motion. First, we removed runs in which 20% or more of the total number of volumes from either their left- or right-hand runs were preceded by framewise head motion >0.75 mm (25% of the voxel size) Euclidean displacement (i.e., $d^2 = \Delta x^2 + \Delta y^2 + \Delta z^2 + [(65\pi/180)^2 \times (\Delta \mathrm{pitch}^2 + \Delta \mathrm{roll}^2 + \Delta \mathrm{yaw}^2)]$ (Mazaika, Whitfield, & Cooper, 2005). Because left-hand and right-hand tapping fMRI data were acquired during separate runs (as described in more detail below), each dataset was treated independently. This procedure removed 3 children and 1 adult from the left-hand dataset and 2 children and 1 adult from the right-hand dataset. Left- and right-hand runs in which fewer than 20% of volumes were preceded by excessive head motion remained for further analysis. From these remaining runs, there were no between-group differences in the average number of volumes removed for the left ($t(26) = -1.75$; $p > .05$) or right ($t(28) = -1.29$; $p > .05$) hand. We next averaged every subject's (a) mean and (b) maximum framewise movement and (c) maximum displacement from the origin across *x*, *y*, and *z* translation and pitch, roll, and yaw rotation directions (restricting these calculations to runs in which fewer than 20% of volumes were preceded by excessive head motion). This produced six movement values per subject per hand, the averages of which are presented for each group and each hand in Table 2. Two-sample *t* tests revealed no significant mean differences between the children and adults for the three measures of translation. However, the groups differed significantly on most measures of rotation for both the left hand and right hand and these were therefore entered into the fMRI analysis as described next.

For each subject, first-level statistics were performed by first applying a temporal high pass filter of 128 s, and then modeling each condition (left hand and right hand) with a convolution of the canonical hemodynamic response function (HRF) and our experimental block design, which we shifted forward by 3 volumes. Fixation was treated as baseline, rather than as a distinct condition. We used an autoregressive (AR 1) model to reduce serial correlations from biorhythms and unmodeled neuronal activity. To account for head motion and changes in the global mean signal as confounds, we created a multiple regression model comprising the 3 rotation motion parameters (please see above), a logical vector to indicate the volumes with >0.75 mm Euclidean displacement head motion (Mazaika et al., 2005), and the global mean signal at each time point. This procedure generated within-subject beta maps for each contrast (Left Hand > Fix and Right Hand > Fix).

To identify within-group activations, we performed second-level statistics operations Left Hand > Fix and Right Hand > Fix for children and adults. To ensure that differences in performance did not drive brain activation, we entered as a covariate of no interest false presses (the sum of superfluous taps for each trial), which correlated with accuracy and response times (please see Section 3.2). To identify areas of activation, we used a height threshold of $p < .001$, and then applied cluster extent thresholds using the CorrClusTh.m algorithm (Thomas Nichols; https://www2.warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/spm/), which yielded an *FWE*-corrected threshold $p < .05$ ($k \geq 101$ for adults Left Hand > Fix and $k \geq 110$ for adults Right Hand > Fix; $k \geq 132$ for children Left Hand > Fix and $k \geq 136$ for children Right Hand > Fix).

To identify between-group activation differences, we performed statistical operations for Children > Adults and Adults > Children for each of the hand tapping contrasts. Again, we entered false presses as a covariate of no interest. Results were generated as described above, with *FWE*-corrected thresholds $p < .05$ ($k \geq 160$ for Left Hand > Fix and $k \geq 164$ for Right Hand > Fix).

While the above analyses are useful for presenting the outcome of children and adults for each hand, we also conducted a full factorial analysis to assess the main effects of Age Group (children vs adults), Hand (left vs right) and their interaction. As such, we performed a 2 × 2 analysis of variance (ANOVA) on whole-brain data, again using false presses as a covariate of no interest. We adjusted our sample such that the same children and adults were used in both left and right hand datasets. This reduced our adult group to $n = 14$ and our children group to $n = 12$. The whole- brain ANOVA was corrected for multiple comparisons to *FWE* cluster-level $p < .05$ with *p*-uncorrected < .001 and $k \geq 180$. To determine the direction of these effects (i.e., whether a cluster showing a main effect of Age Group was driven by greater activation in the adult group), the resulting clusters for each map were subsequently converted into regions-of-interest (ROIs) using MarsBaR (http://marsbar.sourceforge.net), and average percent signal change values for every ROI were extracted from subjects' first level contrasts (Left Hand > Fix and Right Hand > Fix) and then averaged for specific groups depending on the contrast. Visualization of these measures was done using GraphPad Prism 6.

Following second-level statistics, clusters were mapped onto normalized, anatomical images. For all clusters of activation, peak intensities, peak coordinates, and extents were ascertained using SPM8. Coordinates, which SPM8 provided in MNI stereotaxic space, were subsequently transformed into Talairach anatomical space (Talairach and Tournoux, 1988) using the icbm2tal algorithm (Lancaster et al., 2007) included within the GingerALE program, and then labeled as an anatomical region according to the Talairach Daemon (http://www.talairach.org/daemon.html). Functional motor regions (e.g., SM1, SMA, etc.) were labeled using the Human Motor Area Template (HMAT) depicted in axial slices (Mayka, Corcos, Leurgans, & Vaillancourt, 2006). This template was originally derived by implementing the ALE method on 126 fMRI or PET studies involving motor control, and demarcates three main divisions of motor areas, SM1, medial premotor cortex (MPMC), and lateral premotor cortex (LPMC); as well as their subdivisions of primary motor cortex (M1) and primary somatosensory cortex (S1) for SM1, SMA and pre-SMA for MPMC, and PMv and PMd for LPMC. For our reporting, we differentiated the subdivisions of MPMC and LPMC, but not SM1, because most of the studies used in this meta-analysis showed activation in M1 and S1, and those activations registered in a single cluster. This is different from activations in MPMC and LPMC, which often registered in one or the other subdivisions. Probability maps for main and subdivisions represent the likelihood that an activation focus falls within a given area. We reported functional regions based on a 95% probability; that is, if a coordinate fell within the 95% bounds for only one main or subdivision area, we labeled that coordinate as that main or subdivision (with no superscript annotation). Boundary zones (i.e., regions of the map in which main or subdivisions overlapped) manifest U-shaped probabilities, where the nadir represents an equal probability that an activation focus lies in adjacent main or subdivisions. We labeled coordinates in these boundary zones as the main or subdivision with the higher probability. Any coordinates that fell almost perfectly at the nadir were labeled with both names (e.g., pre-SMA/SMA). Any coordinates that fell in one of these boundary zones but overlapped considerably with one particular main or subdivision were labeled according to that main or subdivision, but appended with a superscript: %1 indicated that the boundary was between main divisions (e.g., between SM1 and MPMC) and %2 indicated that the boundary was between subdivisions (e.g., between PMv and PMd). For instance, a label of SMA$^{\%1}$ would indicate that the coordinate is in a boundary zone between the SMA aspect of MPMC and SM1, but mostly in the SMA functional motor region; whereas a label of SMA$^{\%2}$ indicates that the coordinate is in a boundary zone between the SMA and pre-SMA aspects of MPMC, but mostly in the SMA functional motor region. For all clusters, we also visually examined the anterior-, posterior-, medial-, lateral-, ventral-, and dorsal-most voxels of that cluster in MNI space, and then used the same procedure as described above to describe their functional motor area. These regions are described as extensions to the activation peaks reported in the Results section and accompanying tables. All brain maps were visualized using the Mango software package (http://rii.uthscsa.edu/mango/) with the Colin brain template in MNI space (Holmes et al., 1998). All voxels at surface depth ≤10 voxels are visualized at the surface.

3 | RESULTS

3.1 | Participants

After application of our head motion exclusion criteria and removal of datasets due to image degradation or poor image quality, the final groups comprised 17 children and 15 adults, with 14 children (mean age 7.6 ± 0.71 years) and 14 adults (mean age 24.0± 3.0 years) in the left hand dataset and 15 children (mean age 7.5 ± 0.70 years) and all 15 adults (mean age 24.9 ± 2.9 years) in the right hand dataset. Demographic details for the overall groups of 17 children and 15 adults are summarized in Table 1.

3.2 | Behavioral results

In-scanner performance measures, including false presses, percent accuracy, and response times are summarized in Table 3. As expected, for left hand and right hand finger movement, adults relative to children performed significantly fewer false presses, were more accurate, and had faster response times. Also, an ANOVA with our 2 × 2 Age Group × Hand design showed a main effect of Age Group for false presses ($F(48) = 27.4$; $p < .0001$), accuracy ($F(48) = 35.5$; $p < .0001$) and response time ($F(48) = 12.0$; $p < .005$); but no main effect of Hand, or interaction of Age Group × Hand for any measure.

TABLE 1 Subject demographics

	Children	Adults	p value
N	17	15	-
Sex (F/M)	10/7	5/10	-
Age (years)[a]	7.48 (0.66)	24.9 (2.9)	<.0001
Range (years)	6.7–9.1	18.5–28.2	-
Full IQ[a]	124 (11)	117 (9.1)	n.s.

[a]Values are mean and standard deviations.

Given these age-related differences, we entered task performance as a covariate of no interest in our subsequent fMRI analysis. When aggregating performance values for all participants and both hands ($n = 56$) and computing Pearson correlations, we found that the number of false presses was significantly correlated with accuracy ($r = -.89$; $p < .0001$) and response time ($r = .32$; $p < .05$). As such the data for false presses was used as the covariate of no interest in the fMRI analysis.

3.3 | fMRI results

3.3.1 | Within-group maps: Finger tapping versus fixation

For children and adults, whole-brain activation maps for tapping compared with fixation are depicted in Figure 2. A full list of activation peaks corresponding to these contrasts are shown in Table 4, wherein motor regions are specified by anatomical as well as functional labels. For the latter, the presence of %1 or %2 superscript markings appending a particular brain region indicates that the area is in a boundary zone between main divisions (%1) or subdivisions (%2), as described in the Methods.

Children

In children, movement with the left-hand thumb was associated with activity in six clusters: right SM1 (with peak in right postcentral gyrus), right SMA (with peak in right medial frontal gyrus, extending anteriorly into right pre-SMA, and bilaterally into left SMA), right anterior cerebellum, right thalamus, right inferior occipital gyrus, and left middle occipital gyrus.

Tapping with the right-hand thumb elicited activity in six clusters: left SM1 (with peak in left pre-central gyrus), left SMA (with peak in left medial frontal gyrus and extending into right SMA), right putamen, right anterior cerebellum, left thalamus, and left lingual gyrus (Table 4 and Figure 2).

Adults

In adults, tapping with the left thumb was associated with activation in 12 clusters: right SM1 (with peak in right postcentral gyrus), left SMA (with peak in left medial frontal gyrus and extending into right SMA$^{\%2}$ and anteriorly into bilateral pre-SMA), left PMd$^{\%2}$ (with peak in left pre-central gyrus), right and left putamen, left and right anterior cerebellum, right inferior parietal lobe, left supramarginal gyrus, right thalamus, right lingual gyrus, and left cuneus.

Right-hand thumb tapping was associated with activation in 13 clusters: left SM1 (with peak in left post-central gyrus), right pre-SMA$^{\%2}$ (with peak in left medial frontal gyrus and extending bilaterally into pre-SMA$^{\%2}$ and posteriorly into bilateral SMA), right PMd$^{\%1}$ (with peak in right pre-central gyrus), left PMv (with peak in left IFG), left and right putamen, right and left anterior cerebellum, right posterior cerebellum, left insula, left and right middle occipital cortex, and right cuneus (Table 4 and Figure 2).

3.3.2 | Between-group maps: Finger tapping versus fixation

Children > adults

For movement of the left hand, a between-group comparison revealed two clusters where children had relatively more activity than adults: one large cluster in left SMA$^{\%1}$ (with peak in left medial frontal gyrus and extending laterally into left SM1 as well as posteriorly to bilateral precuneus); and a second cluster in the right cingulate gyrus (Figure 3a and Table 5).

Children did not, however, exhibit greater activation than adults for thumb movement of the right hand (Figure 3b).

Adults > children

For left-hand thumb movement, adults exhibited greater activation compared with children in three clusters: right SM1$^{\%1}$ (with peak in right precentral gyrus), right putamen, and left midbrain (Figure 3c and Table 5). Activations in the two former clusters were focused, whereas the latter cluster, centered in left midbrain, extended to ipsilateral putamen and ipsilateral parahippocampal gyrus.

For the right hand, adults exhibited greater activity in two clusters: the first in right pre-SMA (with peak in right medial frontal gyrus extending into left pre-SMA$^{\%2}$ and posteriorly into bilateral SMA$^{\%2}$); and the second in right lateral globus pallidus (Figure 3d).

TABLE 2 In-scanner head motion

Left hand—translation	Children	Adults	p value
Mean interscan (mm)	4.8 (2.8)	3.2 (1.7)	n.s.
Max interscan (mm)	29 (25)	21 (14)	n.s.
Max displ. from origin (mm)	21 (16)	15 (9.4)	n.s.
Left hand—rotation			
Mean interscan (rad)	8.4 (6.8)	3.8 (1.7)	<.05
Max interscan (rad)	63 (55)	27 (16)	<.05
Max displ. from origin (rad)	48 (40)	25 (14)	n.s.
Right hand—translation			
Mean interscan (mm)	4.6 (2.8)	3.2 (2.0)	n.s.
Max interscan (mm)	28 (23)	22 (14)	n.s.
Max displ. from origin (mm)	22 (15)	17 (9.0)	n.s.
Right hand—rotation			
Mean interscan (rad)	7.4 (4.9)	3.5 (1.5)	<.01
Max interscan (rad)	53 (39)	26 (12)	<.05
Max displ. from origin (rad)	44 (29)	23 (9.2)	<.05

Values are mean and standard deviations.
Values were calculated after discarding runs in which 20% or more of the volumes were preceded by >0.75 mm framewise head motion.
All translation measures $\times 10^{-2}$; all rotation measures $\times 10^{-4}$.

TABLE 3 In-scanner performance

	Children	Adults	*p* value
Left-hand false presses	10 (9.6)	0.85 (1.2)	<.005
Left-hand accuracy (% correct)	0.93 (0.058)	0.99 (0.017)	<.005
Left-hand mean response time (ms)	350 (62)	296 (58)	<.05
Right-hand false presses	13 (10)	0.93 (1.4)	<.0005
Right-hand accuracy (% correct)	0.90 (0.056)	0.99 (0.014)	<.00005
Right-hand mean response time (ms)	348 (53)	285 (51)	<.005

Values are mean and standard deviations.
No in-scanner performance data for one adult participant.

3.3.3 | Analysis of variance maps: Finger tapping versus fixation

Main effect of age group (children vs adults)

A main effect of Age Group revealed five clusters in which children differed from adults independent of hand use (left and right combined). Children showed greater activation compared with adults in one cluster: left SM1 (with peak in postcentral gyrus extending medially into bilateral SMA). Here, children showed an increase during thumb tapping, while adults demonstrated a decrease below the control condition (fixation). Adults, meanwhile, showed greater activation compared with children in four clusters: right pre-SMA/SMA[%2] (with peak in medial frontal gyrus, extending into left pre-SMA/SMA[%2]), right lateral globus pallidus, left putamen, and right anterior cerebellum. In all these cases except the cerebellum, adults exhibited robust activity while children exhibited weak activity or, in the case of the globus pallidus, a signal decrease. The cerebellum stayed at baseline for the adults while the children exhibited a signal decrease (Figure 4 and Table 6).

Of note is that the clusters in right pre-SMA and right lateral globus pallidus identified in this main effects analysis to be more active in adults than children, map onto the same areas reported as relatively more active in adults during right finger tapping in the between-group comparison reported in Table 5. Also, the peak of left SM1 identified for children's relatively greater activation in this main effects analysis lies 16 mm lateral, 14 mm posterior, and 0 mm superior to the peak ($Z = 5.15$) of the left SMA reported to be more active in children during left hand finger tapping in the between-group comparison. As shown in Table 5, the left SMA cluster identified in the between-group comparison also extended into left SM1, the subpeak ($Z = 5.06$) of which lies 16 mm medial, 4 mm posterior, and 16 mm superior to the peak of the left SM1 cluster revealed by the main effects analysis, providing the expected consistency between our two analysis approaches. Of note is that these specific differences between children and adults (in both directions) occurred in brain regions ipsilateral to the side of movement.

Main effect of hand (right vs left)

A main effect of Hand (children and adults combined) generated five clusters in which left and right hand movement differed in activation, independent of age group (Table 6). As expected, left thumb tapping generated greater percent signal changes in right SM1 (with peak in right precentral gyrus) and right putamen. Right hand tapping generated greater percent signal changes in left SM1 (with peak in left postcentral gyrus) and right cerebellum, as well as left insula. As can be seen in Figure 5, these signal increases were accompanied by a signal decrease for the other hand, relative to baseline.

Interaction effect of Age Group × Hand

There was an interaction effect between Age Group and Hand used in one cluster: right SM1 (with peak in postcentral gyrus). Here, children and adults showed activation for left (contralateral) finger movement and signal decreases (relative to baseline) for movement made with the right (ipsilateral) thumb; however, for both the left hand movement-induced signal increase and right hand movement-induced signal decrease, the pediatric response was attenuated compared with that of the adults (Figure 6 and Table 6).

Again, these results are consistent with the between-group analysis (Table 5), in that both revealed right SM1 to be more active in adults than children during left hand finger tapping.

4 | DISCUSSION

Despite the abundance and diversity of finger-tapping studies on adults, there remains a paucity of similar research on children. Here, we investigated the brain bases of visually paced, dominant and nondominant hand finger-tapping in children and compared them to those of adults. We found that both children and adults activate a set of cortical and subcortical motor system brain regions including SM1, SMA, and

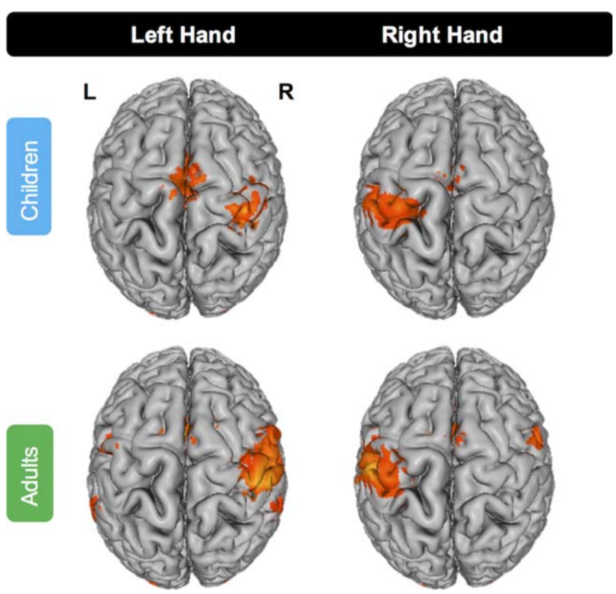

FIGURE 2 Whole-brain activation maps for thumb movements in children and adults. For both children and adults, contrasts of thumb movements made with the left and right hands relative to fixation elicit activations in a network of cortical and subcortical (not shown) brain areas (cluster-corrected threshold of $p < .05$). L, left hemisphere; R, right hemisphere. Table 4 provides the full list of activations revealed by these contrasts

TABLE 4 Locations of whole-brain activation peaks for within-group contrasts for left and right thumb tapping

Group	Anatomical region	Functional motor region	BA	Peak coordinate			k	Z
				x	y	z		
Children	R. postcentral gyrus	SM1	3	34	−26	56	1,178	5.56
Left hand > fix	R. medial frontal gyrus	SMA	6	6	−4	68	1,592	5.02
	R. anterior cerebellum			44	−60	−26	355	5.12
	R. thalamus			20	−20	10	349	4.51
	R. inferior occipital gyrus		17	22	−94	−4	498	5.61
	L. middle occipital gyrus			−28	−92	4	444	4.74
Right hand > fix	L. precentral gyrus	SM1	4	−30	−24	52	1,345	5.38
	L. medial frontal gyrus	SMA	6	−8	−4	52	332	4.11
	R. putamen			22	14	6	413	5.12
	R. anterior cerebellum			8	−56	−12	2,993	5.36
	L. thalamus			−16	−22	8	348	4.74
	L. lingual gyrus		18	−16	−96	−12	852	5.41
Adults	R. postcentral gyrus	SM1	3	44	−26	66	1,842	5.98
Left hand > fix	L. medial frontal gyrus	SMA[%2]	6	−4	4	52	1,221	6.32
	L. precentral gyrus	PMd[%2]	6	−46	−2	40	170	3.95
	R. putamen			24	4	−2	806	4.76
	L. putamen			−26	4	−2	924	4.68
	L. anterior cerebellum			−34	−62	−28	449	5.14
	R. anterior cerebellum			44	−60	−26	442	5.04
	R. inferior parietal lobe		40	60	−44	44	212	3.72
	L. supramarginal gyrus		40	−52	−44	36	170	4.12
	R. thalamus			16	−18	0	242	5.31
	R. lingual gyrus		18	14	−104	−2	408	4.46
	L. cuneus		18	−24	−104	8	124	3.91
Right hand > fix	L. postcentral gyrus	SM1	2	−52	−18	48	1,817	6.07
	R. medial frontal gyrus	pre-SMA[%2]	6	8	10	54	796	5.09
	R. precentral gyrus	PMd[%1]	6	56	2	48	128	7.75
	R. inferior frontal gyrus	PMv	9	50	10	20	174	4.23
	L. putamen			−22	6	0	1,614	4.58
	R. putamen			24	4	10	260	4.06
	R. anterior cerebellum			18	−54	−18	1,338	5.20
	L. anterior cerebellum			−36	−60	−22	238	4.88
	R. posterior cerebellum			12	−66	−44	432	4.26
	L. insula		13	−48	−22	16	245	4.27
	L. middle occipital gyrus		18	−32	−86	6	219	4.11
	R. middle occipital gyrus		37	48	−66	4	112	6.22
	R. cuneus		17	22	−94	10	159	5.36

[%1]% at first level.
[%2]% at second level.

anterior cerebellum for movement with either hand. For movement of the left hand, our between-group comparison revealed, as predicted, areas in which children exhibited greater activation than adults. These were in left SMA (extending into left SM1 and bilateral precuneus) and right cingulate gyrus. But surprisingly there were no areas of more activity in children than adults for right hand movement. Further, there were several brain regions that were more active in adults compared with children. These were in right SM1 during left hand movement and right pre-SMA (extending into left pre-SMA and posteriorly into bilateral SMA) during right hand movement, and basal ganglia structures for movement of either hand.

We also entered our data into a full factorial design and found main effects for Age Group (which were largely consistent with our two-sample t-test between-group comparison) and for Hand. The interaction of Age Group x Hand from our ANOVA revealed that activity in right SM1 is marked by signal increases in both groups when performing a left thumb movement and signal decreases in both groups when performing right thumb movement, but that this pattern was significantly attenuated in children relative to adults.

Together, this investigation provides some evidence in support of the expectation that children engage the brain more during finger tapping movement than adults: Children activated the left SM1 more (as revealed by the between-group analysis for left hand tapping, where the left SMA finding was inclusive of left SM1; and by the main effect of Age Group in the ANOVA). However, against our expectations, numerous regions were more active in adults, including basal ganglia (left putamen and right globus pallidus) and right pre-SMA/SMA (identified by the between-group analysis and main effects for Age Group in the ANOVA). In right SM1, age-related difference interacted with hand use. Next, we discuss these results in the context of the existing literature and address the age-dependent differences and their implications.

4.1 | Within-group results for children and adults

Our findings from the within-group analysis conducted in the adults are consistent with those reported by Witt et al. (2008) in their meta-analysis of right-hand thumb-tapping tasks. While keeping in mind that

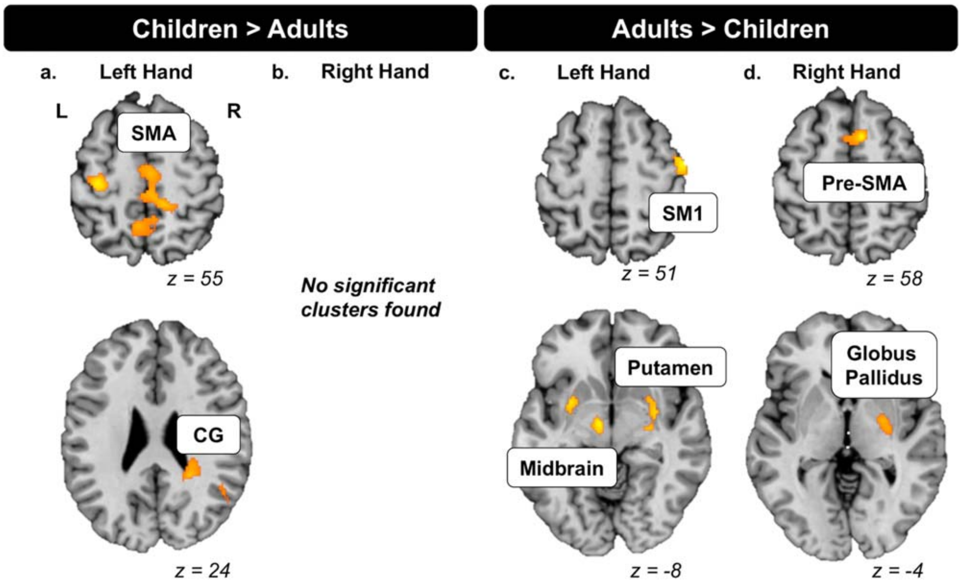

FIGURE 3 Whole-brain activation maps for thumb movements for between-group contrasts. Between-group contrasts identified brain regions more strongly recruited in children (children > adults) for (a) left and (b) right hand movements, or in adults (adults > children) for (c) left and (d) right hand thumb movements (*FWE* cluster-corrected threshold of $p < .05$). L, left hemisphere; R, right hemisphere; SM1, primary sensorimotor cortex; SMA, supplementary motor area; CG, cingulate gyrus. Table 5 provides the full list of activations revealed by these contrasts

the latter was generated from studies using a variety of stimuli (not just visually-paced), both our study and the meta-analysis revealed left SM1, right PMd, right anterior cerebellum, and left anterior cerebellum. Our cluster with a peak in right pre-SMA extends into left SMA, which is consistent with the meta-analysis.

Our pediatric findings are also consistent with previous studies of finger-tapping in children. For instance, like Rivkin et al. (2003), our results showed activations in SM1, SMA, and cerebellum. In addition, Rivkin et al. (2003) reported activity in superior temporal gyrus, while we found activation that Rivkin et al. (2003) did not in occipital cortex, a difference that can be attributed to the auditory (Rivkin et al., 2003) versus visual (the present study) nature of the stimuli used to pace the movement. When considering the study by De Guio et al. (2012), they like us, observed activity in SM1, premotor cortex (SMA specifically in our case), cerebellum, and thalamus. When considering the results reported in pediatric studies of motor tapping in disorders or neural injury, we found similar activations in our children as in the controls of these studies in SM1 (Mostofsky et al., 2006; Roessner et al., 2012, 2013; Vandermeeren et al., 2003), SMA or unspecified area of premotor cortex (Mostofsky et al., 2006, left hand only; Vandermeeren et al., 2003), cerebellum (Mostofsky et al., 2006; Roessner et al., 2012; Vandermeeren et al., 2003), and basal ganglia (Roessner et al., 2012, 2013). However, there are also some differences between areas observed in our study and those reported previously, and these may be the result of differences in statistical thresholds, task complexity, or stimulus modality. Also, our group of children was younger (average age 7) than any of the groups reported to date, all of which fell between average ages of 9 and 14 years.

4.2 | Greater activity in children compared with adults

We had hypothesized that children would exhibit greater activity relative to adults and that such age-related differences may further depend upon whether subjects were using their dominant or nondominant hand. Our analyses initially focused on between-group differences,

TABLE 5 Locations of whole-brain activation peaks for between-group contrasts for left- and right-hand tapping

Group	Anatomical region	Functional motor region	BA	Peak coordinate *x*	*y*	*z*	*k*	*Z*
Children > adults								
Left hand > fix	L. medial frontal gyrus	SMA[%1]	6	−4	−12	70	2,157	5.15
	R. cingulate gyrus		31	24	−44	24	381	4.48
Right hand > fix	No significant results							
Adults > children								
Left hand > fix	R. pre-central gyrus	SM1[%1]	4	50	−8	56	246	4.30
	R. putamen			28	2	−14	292	4.32
	L. midbrain			−8	−12	−8	539	4.35
Right hand > fix	R. medial frontal gyrus	pre-SMA[%2]	6	8	10	54	217	5.14
	R. lateral globus pallidus			26	−6	−2	284	4.17

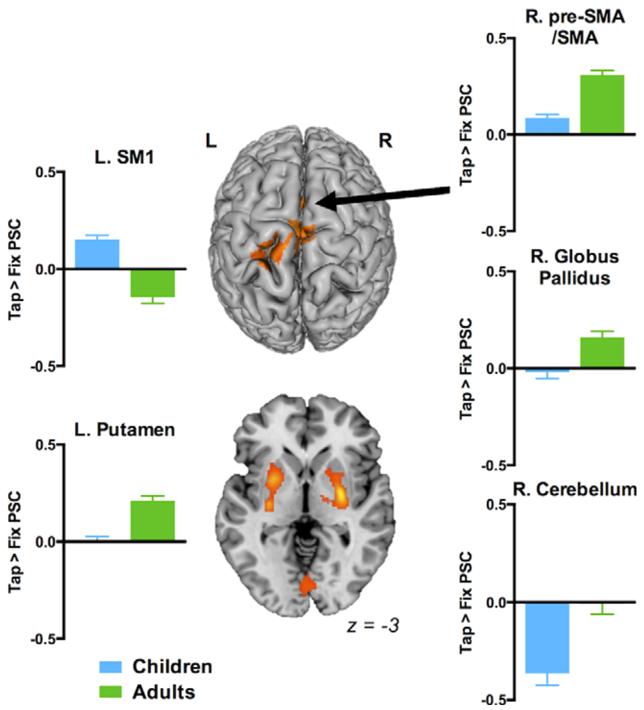

FIGURE 4 Areas revealed by Main Effect of Age Group. Whole-brain ANOVA revealed several brain areas with differential responses to thumb movements. Percent signal change values were extracted from each cluster surpassing a cluster-corrected threshold of $p < .05$ and depicted in the graphs. L, left hemisphere; R, right hemisphere. Table 6 provides the full list of activations revealed by this analysis

mainly so that right hand finger tapping, the most widely used task in the field, could be directly contrasted in children and adults. However, to determine whether the age-related differences depend on the hand used (left versus right), we also entered the data into a full-factorial design. As the results from the between-group comparisons and the ANOVA are interrelated, both will be discussed here and organized around cortical and subcortical regions.

4.2.1 | Left SM1

One of only two regions to emerge from the between-group comparison as more active in children than adults was left SMA with extension into left SM1 (the other region was right cingulate gyrus; Table 5), which emerged during left hand finger tapping. Meanwhile, a similar cluster with a peak in left SM1, and extending into left SMA, emerged from the ANOVA as a main effect of Age Group, as the only area to be more active in children than adults across the two hands combined (Figure 4 and Table 6). We address the SM1 component of this cluster here and the SMA component below. The location of the SM1 region derived from the main effect of Age Group analysis (peak at $x = -20$, $y = -26$, $z = 70$ MNI) is situated medial and superior to the primary motor cortical representation found for right hand thumb movement in the children (−30, −24, 52) and adults (−52, −18, 48); and also for that reported in the literature for right-hand thumb movement in a high-resolution fMRI study by Dechent and Frahm (2003): $x = -39$, $y = -23$, $z = 50$.

As indicated by Figure 4, the age-related differences in this region might be driven by signal decrease (relative to the fixation baseline) in adults. However, it should be noted that the main effect of Age Group was computed from left and right hand tapping data. When examining PSC separately for each hand, we observed qualitative signal decreases relative to baseline for the left and right hands in adults and qualitative signal increases relative to baseline in the children. In addition, it has to be noted that the finding is in a medial region of SM1 that was not actually found to be activated in the within-group analysis for either children or adults. Therefore, the greater activity in this region in children would likely not have emerged were it not for the signal decrease in adults. Signal decreases in adults in this region would make sense as it falls outside the putative hand area for left and right hand finger movements.

Developmental models have been proposed to explain greater activation or more distributed activation patterns in children compared with adults (Poldrack, 2010). For instance, activation of fewer brain areas in adults compared with children may be attributed to “neural efficiency” of adults or “scaffolding” in children, whereby some certain brain regions in children support performance on multifarious tasks, prior to more specialized computations of regions in adult brains (Poldrack, 2010). Further research, preferably longitudinal in nature, would be needed to determine which model best explains developmental changes in the motor system.

4.2.2 | SMA

Returning to the original fMRI study in children by Rivkin et al. (2003), their bimanual externally paced condition resulted in activation in bilateral posterior superior temporal gyrus, SM1, SMA, and cerebellum. The authors, who did not include adults in the study, suggested that the SMA was unique to children. We did find that caudal SMA (identified as an extension of a cluster with peak in left SM1 in the main effect of Age Group, combining both left and right hand runs) was more activated in children than adults. However, our results do not confirm the theory by Rivkin et al. (2003), because we found SMA to be active in both groups for movement of either hand. Further, we found that other aspects of SMA (specifically pre-SMA/SMA) were less active in children compared with adults.

Medial premotor cortex is thought to be involved in the initiation of movement (Nachev, Kennard, & Husain, 2008). Generally speaking, by comparison with lateral premotor cortex, SMA has been associated more with internally triggered finger movement (Mushiake, Inase, & Tanji, 1991), but it is also involved in externally-paced movement (Cunnington, Windischberger, Deecke, & Moser, 2002). In addition, an anterior–posterior continuum is thought to mark medial premotor cortical areas, with more anterior pre-SMA recruited for relatively higher-order tasks and SMA proper recruited for lower order tasks (Nachev et al., 2008; Picard and Strick, 1996). The greater reliance by children on caudal SMA, a brain area thought to subserve lower level processing, for accomplishing finger movements may be surprising, as one might expect an irregularly paced finger-movement task to be relatively difficult for children, necessitating recruitment of anterior aspects of SMA (or pre-SMA). On the other hand, it is possible that such recruitment of

TABLE 6 Locations of ROI peaks derived from ANOVA

Anatomical region	Functional motor region	BA	Peak coordinate x	y	z	k	Z
Main effect of age group							
Children > adults							
L. postcentral gyrus	SM1	3	−20	−26	70	544	4.72
Adults > children							
R. medial frontal gyrus	pre-SMA/SMA[a]	6	6	8	56	336	5.41
R. lateral globus pallidus		28	−8	−4	1,075	5.76	
L. putamen			−28	4	−6	1,223	5.28
R. anterior cerebellum			4	−68	4	350	4.40
Main effect of hand							
Left hand > right hand							
R. precentral gyrus	SM1	4	36	−22	50	2,164	inf
R. putamen			32	−10	−2	197	5.05
Right hand > left hand							
L. postcentral gyrus	SM1	2	−48	−18	54	2,051	7.78
R. anterior cerebellum			16	−52	−22	1,010	6.40
L. insula		13	−40	−18	10	363	4.80
Interaction effect of Age Group × Hand							
R. postcentral gyrus	SM1	3	48	−14	58	188	4.19

[a]Equally likely at 0%.

anterior SMA proper or pre-SMA is prohibitive in younger children, or is unnecessary due to other brain areas (e.g., left SM1) compensating. These findings also overlap, in part, with those of De Guio et al. (2012), who studied children and adults on an internally paced, right-hand finger-tapping task and observed greater activations in children compared with adults in bilateral SM1 (as well as bilateral cerebellum, occipital cortex, left premotor cortex and middle temporal gyrus, as well as right thalamus). Our own study, however, did not identify any regions where there was more activity in children than adults for right hand finger tapping (between-group analysis, Table 5).

4.3 | Greater activity in adults compared with children

4.3.1 | Right SM1

Our between-group comparison revealed greater activity in adults than children in right SM1 for left hand movement. When examining the within-group brain maps, activation in right SM1 in children is focused, while that in adults is distributed, extending ventro-laterally. Indeed, it is this ventro-lateral extension in the adult within-group map that emerged as greater activation in adults compared with children.

Further clues to explain effects in right SM1 may lie in the result that the same area was brought out in the ANOVA as an interaction of Age Group by Hand. Specifically, this analysis revealed that during left hand finger tapping, right SM1 is more active in adults than children, and during right hand finger tapping, it exhibits a weaker signal decrease in children than adults. This finding is important because it represents an age-related effect that is dependent upon whether the right or left hand is used. Depending upon fMRI task design, this could have substantial implications for developmental cognitive studies in which subjects complete tasks with both hands.

The literature in adult studies shows that signal decreases in SM1 ipsilateral to the side of movement are common for motor tasks (Allison, Meador, Loring, Figueroa, & Wright, 2000; De Guio et al., 2012; Hamzei et al., 2002; Hayashi et al., 2008; Newton, Sunderland, & Gowland, 2005; Nirkko et al., 2001; Stefanovic, Warnking, & Pike, 2004) and our data showed that in right SM1 this effect is stronger in adults than children for movement of the right hand (Figure 6), a finding consistent with De Guio et al. (2012). One possible explanation for this weaker signal decrease in children compared with adults (or signal increases in children when adults are exhibiting signal decreases, as observed for left SM1/SMA; Figure 4) may lie in transcallosal inhibition (TI). In adults, TI emerges when primary motor cortex (M1) contralateral to the movement (e.g., left M1 during right hand movement) inhibits M1 ipsilateral to the movement (i.e., right M1) (Boroojerdi, Diefenbach, & Ferbert, 1996; Daskalakis, Christensen, Fitzgerald, Roshan, & Chen, 2002; Duque et al., 2007; Ferbert et al., 1992; Gerloff et al., 1998; Meyer, Röricht, Gräfin von Einsiedel, Kruggel, & Weindl, 1995; Meyer, Röricht, & Woiciechowsky, 1998; Netz, Ziemann, & Homberg, 1995; Stinear, Walker, & Byblow, 2001). Findings from transcranial magnetic stimulation studies suggest that TI begins to develop after age 5 (Heinen et al., 1998) and does not completely develop until age 10 (Muller, Kass-Iliyya, & Reitz, 1997), roughly 2.5 years after our children's mean age (7.48 years). It is possible that many of the TI connections have yet to mature; however, interpretations of BOLD deactivations should be made with caution. In short, while the overall pattern for this region is similar in children and adults, it is substantially attenuated in children.

4.3.2 | Basal ganglia

Our results revealed subcortical areas that differed in activation between children and adults. The between-group analysis revealed that tapping with either hand elicited greater activation in adults than children in lentiform nucleus (for left hand movement, right putamen, and left putamen as an extension from midbrain; for right hand movement, right globus pallidus). The ANOVA revealed a main effect of Age Group

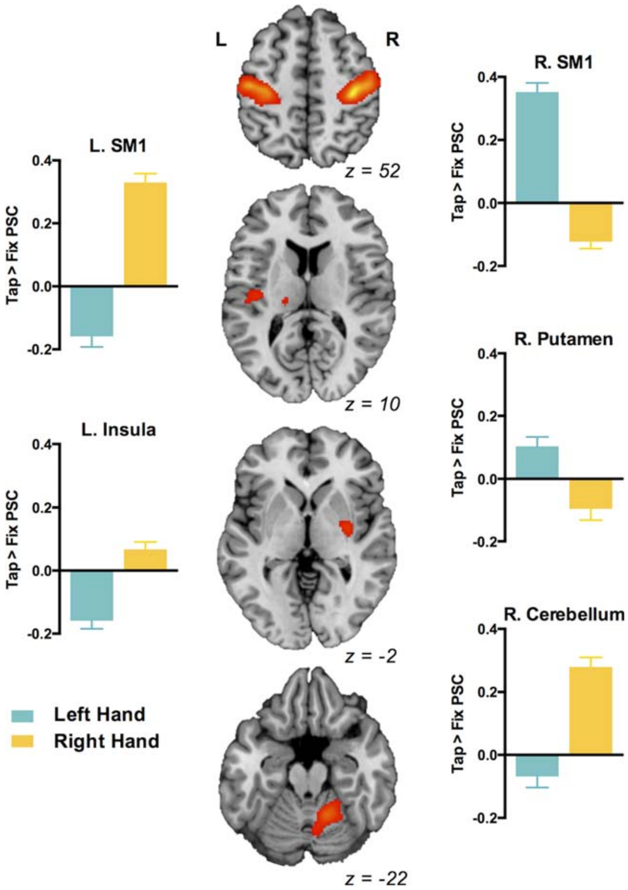

FIGURE 5 Areas revealed for Main Effect of Hand. Whole-brain ANOVA revealed several brain areas with differential responses to thumb movements. Percent signal change values were extracted from each cluster surpassing a cluster-corrected threshold of $p < .05$ and depicted in the graphs. L, left hemisphere; R, right hemisphere. Table 6 provides the full list of activations revealed by this analysis

in left putamen and right globus pallidus, due to greater activations in adults. These observations dove-tail with age-related structural differences observed in previous studies. For example, bilateral lentiform volume, relative to total brain size, has been shown to decrease from childhood to adulthood (Sowell, Trauner, Gamst, & Jernigan, 2002) and striatal gray matter density, as measured by voxel-based morphometry, decreases through adolescence (Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). These reductions may be associated with maturation processes, including reductions in synaptic density and neuronal loss, which occur over development (Huttenlocher, 1979). It is possible that these decreases in size are accompanied by increases in activity. Further, diffusion tensor imaging has revealed a positive correlation between age and fractional anisotropy in the basal ganglia for subjects aged 6–19 years (Barnea-Goraly et al., 2005). Thus, the activation pattern observed in the basal ganglia is likely associated with structural differences between children and adults.

4.4 | Hand-related differences

As expected, the ANOVA revealed main effects of Hand, favoring left SM1 for movement of the right hand and right SM1 for movement of the left hand. The right putamen activated for movement of the left hand while right anterior cerebellum was recruited for movement of the right hand. As mentioned above, signal decreases in ipsilateral SM1 are commonly observed in motor tasks (Allison et al., 2000; De Guio et al., 2012; Hamzei et al., 2002; Hayashi et al., 2008; Newton et al., 2005; Nirkko et al., 2001; Stefanovic et al., 2004). However, also observed in previous finger-tapping studies are signal increases in additional motor cortical areas ipsilateral to the movement for the nondominant hand (Cramer et al., 1999; Hutchinson et al., 2002; Kawashima et al., 1993; Mattay et al., 1998; Verstynen, Diedrichsen, Albert, Aparicio, & Ivry, 2005). Here, our main effect of Hand results showed that SM1 was deactivated during movement of the ipsilateral thumb for either left or right hand. However, it is possible that certain areas, perhaps more anterior premotor regions, were active during movement of both hands, and thus would not be revealed by a main effect of Hand. Examining the within-group maps, adults showed activation in ipsilateral PMd for movement of either hand. The findings in ipsilateral PMd activity are consistent with previous studies (Cramer et al., 1999; Verstynen et al., 2005). In right-handed subjects, these ipsilateral activations have been reported to be stronger for left compared with right hand single finger tapping (Verstynen et al., 2005).

4.5 | Other implications of the results

For cognitive tasks, many use a button press to indicate the outcome of a cognitive decision. While most use a motor response for both the experimental and the active control task, not all do. When such an experimental design is used to compare children with adults, it is assumed that the activity induced by the motor task is not age-

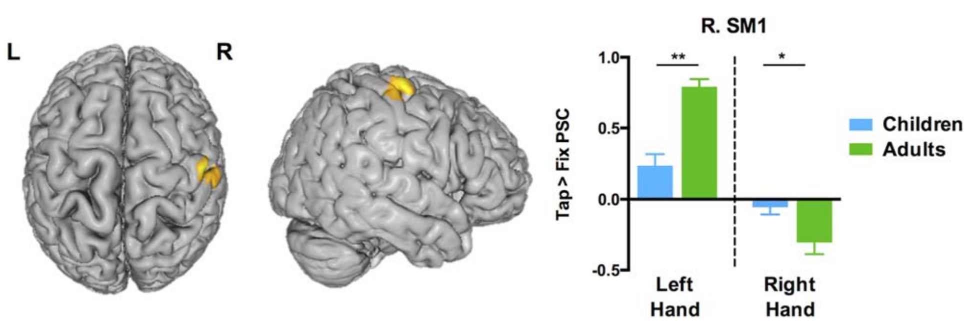

FIGURE 6 Area revealed for Interaction Effect of Age Group × Hand. Whole-brain ANOVA revealed a significant interaction effect of Age Group × Hand in right SM1. $^{*}p < .05$, $^{**}p < .001$

dependent; however, this has never been tested directly. Here, we show that children differed from adults independent of hand use (left and right combined) in left SM1 (extending into bilateral SMA; children > adults) and in right pre-SMA/SMA (extending into left pre-SMA/SMA), right lateral globus pallidus, left putamen, and right anterior cerebellum (adults > children) and dependent on hand use in right SM1 (adults > children for left hand finger movement and children > adults for right hand finger movement).

4.6 | Conclusion

We studied the functional neuroanatomy of the motor system in children and showed that, like adults, children activate SM1, SMA, occipital cortex, and anterior cerebellum for irregularly, visually paced, left and right hand finger-tapping. Using a full-factorial design, we found that at the cortical level, children exhibited relatively greater activation in left SM1 extending into bilateral SMA and adults exhibited greater activation in right pre-SMA/SMA extending into left pre-SMA/SMA. Subcortically, adults recruited basal ganglia structures more strongly, perhaps reflecting a developmental shift to more subcortical processing in adulthood. Interestingly, both pre-SMA/SMA and basal ganglia are associated with initiation of movement and motor control, respectively, and both with complex movements, suggesting a different role for these in developed motor control of voluntary movement in children and adults. Last, the interaction of Age Group × Hand revealed that in right SM1 both groups show a pattern of signal increase (i.e., above fixation baseline) during left finger tapping and signal decrease (i.e., below fixation baseline) during right finger tapping and that this pattern is attenuated in children. These findings provide a reference for the study of developmental disorders with associated motor impairments.

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